

Evaluating community impacts of ocean acidification using qualitative network models

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ABSTRACT: We applied Qualitative Network Models (QNMs) to evaluate the potential community effects of ocean acidification (OA) in a major shellfish-producing estuary (Willapa Bay, Washington). QNMs are well-suited to data-limited systems and only require information on the sign (+, −, 0) of the interactions between species. We examined qualitative predictions of community responses to 13 different OA scenarios that corresponded to 3 broad categories of hypothesized OA effects: (1) increased primary productivity, (2) reductions in bivalve populations, and (3) enhanced predation interactions between bivalves and their crab and gastropod predators. The cultivated bivalve Manila clam tended to respond negatively across scenarios, while primary producers (phytoplankton and eelgrasses) and Chinook salmon tended to respond positively. Trade-offs between species were also assessed: Manila clam and Pacific oyster were predicted to decrease and increase, respectively, when direct OA effects were limited to eelgrasses and the reverse occurred when phytoplankton alone was stimulated by OA. We analyzed the QNMs to identify key linkages that influenced the sign outcome of community members and might therefore warrant future quantitative study. QNMs may be particularly relevant to researchers as a simple method for identifying conditions under which the sign response of species to OA, as inferred from single-species OA experiments, will likely hold in the wild. Given data limitations in most systems, QNMs are a practical alternative or complement to data-intensive quantitative approaches and may help accelerate our understanding of the community-wide effects of OA in marine systems.

KEY WORDS: Community interactions · Indirect effects · Loop analysis · Aquaculture · Shellfish · Global warming · Climate change

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INTRODUCTION

Fundamental shifts in ocean carbonate chemistry that result in lower pH, higher CO₂ partial pressure (pCO₂), and reduction in the saturation state of seawater with respect to calcium carbonate minerals,

are predictable outcomes of increasing atmospheric concentrations of CO₂ due to human activities (termed 'ocean acidification', OA; Feely et al. 2009, Orr 2011). In contrast, our understanding of the potential impacts of these changes on organisms and ecosystems is far from complete, and the issue

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remains the focus of intense research. To date, studies of the biological effects of OA have predominantly assessed the direct effects of increasing $p\text{CO}_2$ on organisms, and suggest some general patterns such as increased performance in certain primary producers and decreased performance in organisms that grow calcified body structures (Kroeker et al. 2013a). However, there is considerable variation in species responses within functional and taxonomic groups, which limits our ability to extrapolate experimental results to unstudied species (Dupont et al. 2010, Hendriks et al. 2010, Harvey et al. 2013, Kroeker et al. 2013a).

Identifying the direct effects of OA on organisms is a necessary and important first step, but understanding the likely response of species to OA also requires consideration of the community context in which they exist. Indirect interactions strongly influence community dynamics (Wootton 1994), and some empirical evidence suggests interspecific interactions can play important roles mediating OA effects (Connell et al. 2013, Falkenberg et al. 2013). Changes in the performance of predators, prey, or competitors can alter the strength of ecological interactions, which may amplify, neutralize, or even reverse the direct effects of OA on individual species. Thus, many authors have cautioned against drawing inferences from results of single-species experiments to the potential performance of wild populations under OA (Connell et al. 2013, Kroeker et al. 2014, Gaylord et al. 2015).

Shifts in community structure due to elevated CO_2 have been observed in several field (e.g. Hall-Spencer et al. 2008, Wootton et al. 2008, Kroeker et al. 2013b, Fabricius et al. 2014) and experimental studies (e.g. Hale et al. 2011, Peck et al. 2015). However, given the broad spatial and temporal scales over which communities operate, predictions of community-wide responses to OA require the use of models that can synthesize information on direct OA effects and also capture important indirect effects that emerge from the network of species interactions (Le Quesne & Pinnegar 2012, Russell et al. 2012). Although ecosystem-scale models vary in complexity and approach (Plagányi et al. 2011), their application to OA has informed us on how changes in productivity in some species may have cascading effects on other trophic groups, and potentially exacerbate the impacts of other stressors (Kaplan et al. 2010, Ainsworth et al. 2011, Griffith et al. 2012, Morris et al. 2014). Quantitative ecosystem models, however, have immense data requirements that make them difficult to parameterize in regions that are data-poor

(Plagányi & Butterworth 2004). In addition, results can be sensitive to small parameter errors and uncertainty in model structure (Hill et al. 2007, Link et al. 2012).

Qualitative network models (QNMs) offer a useful and complementary alternative to data-hungry quantitative approaches. The qualitative modeling approach was first developed by Levins (1974) and Puccia & Levins (1985) and allows formal analysis of the contribution of feedback properties to system dynamics based only on the sign (+, -, 0) of the pairwise interactions of variables composing a system. Although QNMs do not allow for numerical prediction, they can qualitatively predict system responses to external perturbations (Puccia & Levins 1985, Levins 1998). Further, QNMs can account for interspecific interactions as well as interactions between species and abiotic variables, or variables that may be difficult or impossible to measure (Puccia & Levins 1985, Levins 1998). The flexibility of QNMs has made them an appealing tool for a broad range of applications in ecology, including prediction of the community-level effects of eutrophication (Lane & Levins 1977, Carey et al. 2014), habitat disturbance (Dambacher et al. 2007), fishing (Ortiz & Wolff 2002, Metcalf 2010), species invasions and eradications (Castillo et al. 2000, Raymond et al. 2011), shifts in climate modes (Ortiz et al. 2002), and global warming (Dambacher et al. 2010, Melbourne-Thomas et al. 2013).

QNMs are a particularly promising tool for evaluating the effects of OA because the consequences of OA on individual species or functional groups can often only be characterized qualitatively. In most studies, survival or reproduction rates under OA conditions are measured in artificial laboratory conditions and the degree to which they may correspond to rates in the wild is highly uncertain. Further, experimental findings or field evidence may imply change in survival (e.g. altered predator avoidance behavior, sensory ability, shell strength, growth, or metabolism), but quantitative functions relating response variables to a population's vital rates are usually unknown. QNMs can provide a framework for synthesizing the direct qualitative effects of OA on individual species and for analyzing potential outcomes at the community level. Practical applications of QNMs to OA may include evaluation of potential tradeoffs between species and the screening of multiple scenarios to identify species that are consistently and adversely affected by OA (e.g. Carey et al. 2014, Reum et al. 2015).

Here, we demonstrate the value of QNMs for examining potential impacts of OA on ecological

communities by building a model for Willapa Bay, Washington, a major shellfish-producing estuary on the USA west coast. Specifically, we built a QNM of Willapa Bay to simulate 3 potential impacts of OA: increased primary production, reduced production of bivalves, and enhanced predation by crabs and gastropods on bivalves. We used the models to (1) qualitatively predict potential community impacts of OA and (2) identify individual interactions that are most influential in propagating OA through the community.

MATERIALS AND METHODS

Study site

Willapa Bay is a productive, large (260 km²) estuary that has supported commercial shellfish aquaculture for over a century (Feldman et al. 2000). The estuary is an important region for the cultivation of the non-native Pacific oyster *Crassostrea gigas* and supplies ~10% of all oysters consumed domestically in the USA (Ruesink et al. 2006). In addition, the introduced Manila clam *Venerupis philippinarum* is also intensively cultivated. Apart from cultivated shellfish, the estuary also supports a diverse ecological community, wild fisheries for Dungeness crab *Cancer (Metacarcinus) magister*, and provides habitat to species of management and conservation concern including threatened fishes (Chinook salmon *Oncorhynchus tshawytscha*, green sturgeon *Acipenser medirostris*) and migratory waterfowl (Black brant *Branta bernicla nigricans*). During the spring and summer months, northerly winds result in the upwelling of nutrient-rich waters along the open coast which, in turn, promote high rates of primary production and dense standing stocks of phytoplankton that circulate into the estuary, supporting secondary production (Hickey & Banas 2003, Banas et al. 2007).

Like many other estuarine systems (Borges & Abril 2011, Duarte et al. 2013), $p\text{CO}_2$ in Willapa Bay ranges widely (~300 to 4000 μatm) and varies spatially, with the highest values occurring up-estuary and in association with low-salinity waters (Ruesink et al. 2015). Short-term variability (hours to months) in carbonate chemistry is influenced by freshwater inputs, rates of photosynthesis, coastal upwelling conditions, and processes that influence the abundance and remineralization of organic material (Ruesink et al. 2015). However, marine carbonate chemistry conditions in Willapa Bay are also partly influenced by atmos-

pheric $p\text{CO}_2$ levels, as are conditions in adjoining coastal waters (Feely et al. 2008). Consequently, $p\text{CO}_2$ levels in Willapa Bay are likely to increase over the long-term (years to decades) with increasing atmospheric $p\text{CO}_2$, assuming that watershed processes and community metabolism also remain stable over time (Borges & Abril 2011, Duarte et al. 2013).

Qualitative network models

QNMs represent formal conceptual models of how variables within an ecosystem interact. The structure of the system can be represented using a special type of graph known as a signed digraph, where linkages (graph edges) connect system variables (graph vertices) and represent the sign of direct effects (Puccia & Levins 1985). The signed digraphs are mathematically equivalent to a matrix of interactions that, in ecology, typically represent food web interactions. However, the approach is general and linkages can also represent any type of ecological interaction (e.g. competition, facilitation) or interactions between species and other kinds of variable (e.g. abiotic, social, economic).

The analysis of QNMs is based specifically on analysis of the community matrix (Levins 1974, Puccia & Levins 1985). A fundamental premise of the approach is that the per capita change in a species or the level of a non-species variable can be described as a continuous function of some or all of the other variables in the system. Specifically, the approach assumes that the dynamics of n interacting variables can be represented as a set of ordinary differential equations, where for each variable x ($i = 1, 2, \dots, n$):

$$\frac{dx_i}{dt} = f_i(x_1, x_2, \dots, x_n; c_1, c_2, \dots, c_n) \quad (1)$$

That is, the growth rate of variable x_i is a function of the levels of some or all variables in the system, and usually itself, and a set of growth parameters c . For species variables, their c parameters may correspond to birth, death, or immigration rates. The interaction coefficient a_{ij} indicates the effect of a small change in the level of variable j on the level of variable i , and is defined as the partial derivative $a_{ij} = \partial f_i / \partial x_j$ evaluated at the equilibrium (Puccia & Levins 1985). Species interactions can be nonlinear in form, but are assumed to be well-represented by a linear approximation near equilibrium abundance (Bender et al. 1984). The community matrix \mathbf{A} is composed of elements a_{ij} . Predicted changes in system equilibrium abundances resulting from long-term effects of a

press perturbation (defined as a sustained shift in the per capita growth rate of a population or level of a non-species variable) are obtained from the negative of the inverse community matrix ($-\mathbf{A}^{-1}$).

Quantitative estimates of a_{ij} are often difficult to acquire in ecological systems and quantitative predictions may be highly sensitive to small errors in a_{ij} (Yodzis 1988, Dambacher et al. 2002). As an alternative, the network can be specified qualitatively using only the sign (+, −, 0) of the interactions. Doing so permits inclusion of variables that may be difficult to measure and enables qualitative prediction of the response of community members to press perturbations (Levins 1974, Puccia & Levins 1985). If system feedback loops are of the same sign, the predicted sign response is unambiguous. However, in even moderately complex ecological systems, species may be affected by multiple feedback loops of opposite sign. As a result, ambiguity in sign response may arise (i.e. the sign response may be indeterminate; Dambacher et al. 2003).

We adopted a probabilistic QNM approach where the interaction strengths were simulated from a specified distribution of potential values. The method enables prediction of the sign outcome of system variables to a press perturbation as well as estimation of the level of sign determinacy (Raymond et al. 2011, Melbourne-Thomas et al. 2012). Further, sign determinacy calculated under the probabilistic approach can readily incorporate model structural uncertainty (Raymond et al. 2011, Melbourne-Thomas et al. 2012). In the context of QNMs, structural uncertainty refers to linkages whose existence in the network is uncertain, but if they do occur their sign is known (Raymond et al. 2011).

Under the probabilistic approach, a QNM was first specified and uncertain linkages were noted. The following simulation protocol was then carried out: (1) a community matrix configuration was generated by sampling uncertain links from a binomial distribution; (2) the interaction strengths of the community matrix were then drawn from a uniform distribution that spanned 2 orders of magnitude (0.01 to 1), and all negative self-effect interaction coefficients were drawn from a uniform distribution spanning 0.25 to 1 (Raymond et al. 2011); (3) the community matrix was checked against system stability criteria (Melbourne-Thomas et al. 2012) and if stable, the responses of the community to the press perturbation were calculated. If unstable, the community matrix was discarded and a new community matrix was drawn and the simulation procedure commenced again. For each press scenario, the sign responses from 10^4 sta-

ble community matrices were obtained. Sign determinacy is conveyed by the degree of consistency in sign responses across simulated community matrices: high consistency corresponds to high sign determinacy. We note that the community interaction matrices could be constrained further to only those that are able to reproduce responses of community members to well-understood system perturbations based on observations from time series data (Raymond et al. 2011), but for Willapa Bay, such validation criteria were not available.

The Willapa Bay model

The focus of our modeling was on the potential impact of OA on species of management or conservation concern. Therefore, we focused on identifying interactions among these species and included other key functional groups. The species included in the model and the nature of their interactions were informed by a literature review and consultation with commercial shellfish growers and scientists with expertise on the ecology of Willapa Bay. In cases where species were functionally similar, taxa were grouped to simplify the model. For instance, the variables 'small fishes', 'zooplankton' and 'phytoplankton' represent taxonomically diverse groups, but we assumed that the ecological function of species composing each group were similar. In addition, we grouped most small-bodied benthic invertebrates into one of 2 classes: those that associate with structurally complex habitats (eelgrass beds and oyster beds) and those that prefer mud or unstructured habitat (Ferraro & Cole 2007). Although differences in benthic invertebrate assemblages among complex habitat types in Willapa Bay have been observed (e.g. Hosack et al. 2006), we made the simplifying assumption that they play similar functional roles and could be utilized by similar predator assemblages. The model is 'minimal realistic' in that we sought to include enough detail to capture the interplay of direct and indirect interactions that influence aquaculture and community-wide dynamics but also minimize the number of variables in the model to aid interpretability and reduce prediction uncertainty (Fulton et al. 2003).

Model components and linkages are shown in Fig. 1 and details of the specific type of ecological interaction represented by each linkage are available in Table S1 in the Supplement at www.int-res.com/articles/suppl/m536p011_supp.pdf. Following Raymond et al. (2011), we also included negative

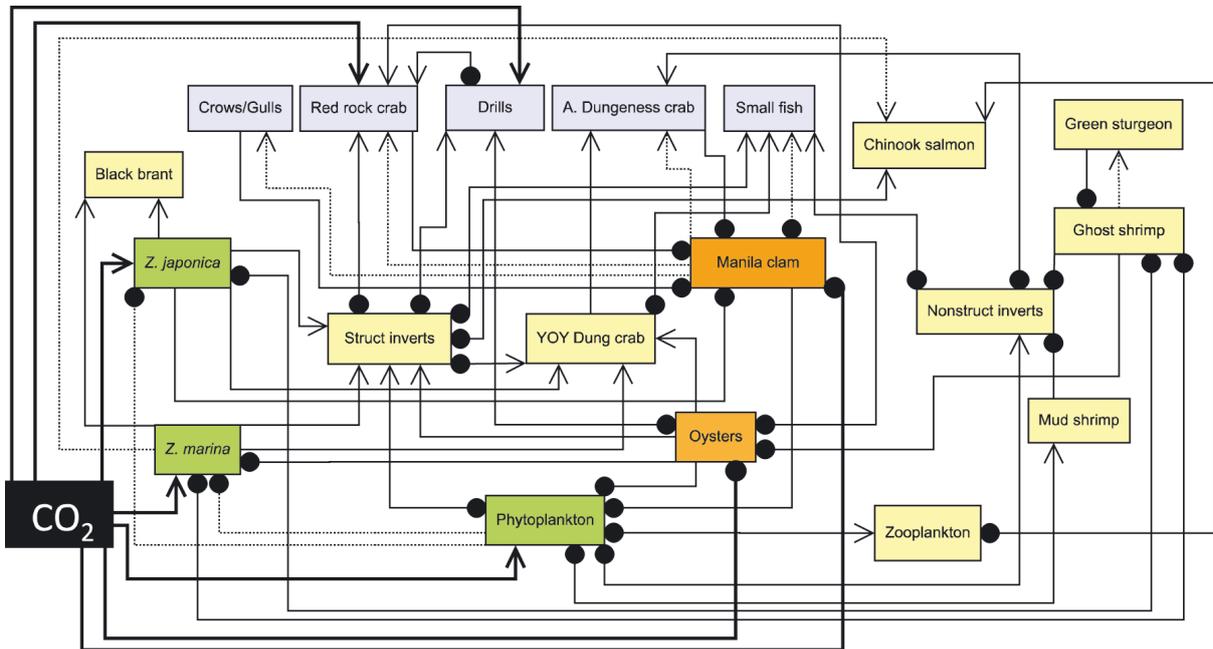


Fig. 1. Qualitative interaction network for Willapa Bay, Washington. Lines terminated with arrowheads indicate a positive influence; those terminated with a dot indicate a negative influence. Lines that terminate with an arrowhead at one end and a dot at the other end indicate predator–prey relationships. Dotted lines indicate interactions that are not well understood. Interactions between CO_2 and community members that correspond to different ocean acidification scenarios are in **bold**. All community members have a limiting (negative) self-interaction, but for clarity these are not shown. Green: primary producer; orange: bivalves; purple: bivalve predators; yellow: all other community members. A.: adult; Nonstruct inverts: nonstructure invertebrates; Struct inverts: structure invertebrates; YOY Dung crab: young-of-the-year Dungeness crab; *Z. japonica*: *Zostera japonica*; *Z. marina*: *Zostera marina*

self-effect links for all biological variables in the model (not shown in Fig. 1). Negative self-effects, which represent self-dampening processes that correspond to density-dependence or potential control of population dynamics by variables outside the modeled system, are essential to system stability (Puccia & Levins 1985). The presence of some linkages in the system was unclear, reflecting uncertainty in model structure. These linkages were noted and structural uncertainty was incorporated into the simulation analysis.

Ocean acidification scenarios

The biological processes that OA can influence at the individual and population levels are known to be diverse, but are only partially understood. Given this state of knowledge, our intention was not to evaluate all OA effects, but rather to explore the potential role of community interactions in mediating and propagating 3 commonly discussed OA impacts, as follows:

(1) *OA will stimulate primary production.* Increased $p\text{CO}_2$ can cause a fertilization effect that ele-

vates photosynthetic rates, leading to higher growth rates among phytoplankton and eelgrass (Thom 1996, Zimmerman et al. 1997, Palacios & Zimmerman 2007, Koch et al. 2013, Kroeker et al. 2013a).

(2) *OA will decrease bivalve production.* OA may reduce bivalve production directly by reducing larval survival or adversely affecting variables that influence survival like individual growth, development, and calcification rates (Kurihara et al. 2007, Barton et al. 2012, Hettinger et al. 2012, Timmins-Schiffman et al. 2013, Waldbusser et al. 2013). These effects in turn may reduce the density or viability of natural or outplanted sets (Barton et al. 2012, Hettinger et al. 2013).

(3) *OA will alter predator–prey interaction strengths.* OA may cause declines in bivalve shell strength, thickness, or size, resulting in higher vulnerability to predators, thereby strengthening predation interactions (Kroeker et al. 2014, Sanford et al. 2014).

The QNM included the variable ' CO_2 ', which represents carbonate chemistry conditions. It was linked to species in a manner that corresponded to the different hypothesized OA effects (Fig. 1). For the first

hypothesis, we examined model scenarios in which CO₂ was linked to individual functional groups or species of primary producers (phytoplankton; the eelgrasses *Zostera marina* and *Z. japonica*) and another in which CO₂ was linked to all primary producers simultaneously (Scenarios 1a–e; Table 1). For the second hypothesis, CO₂ was linked to individual bivalve species (Pacific oyster, Manila clam) and to both species simultaneously (Scenarios 2a–c; Table 1). In the third hypothesis, we focused on the potential for enhanced predatory interactions at 2 points in the model: the predation linkages between (1) drills (predatory gastropods) and Pacific oyster (prey) and (2) red rock crab (predator) and Pacific oyster (prey). To simulate enhanced predation due to OA, positive linkages extending from CO₂ to the predator and negative linkages extending from CO₂ to the prey were added (Dambacher & Ramos-Jiliberto 2007). We examined model scenarios where enhanced interactions were considered individually (Scenarios 3a,b) and in combination (Scenario 3c; Table 1). Last, we evaluated community responses in scenarios that combined the first hypothesis with the second and third hypotheses to evaluate whether multiple OA impacts could reinforce or reverse potential community outcomes (Scenarios 4a,b; Table 1).

For each OA scenario, CO₂ was pressed and shifts in community equilibrium abundances were calculated using the simulation protocol described in ‘Materials and methods: Qualitative network models’. The predicted response of the community corresponds to outcomes resulting from some increment in CO₂, the level of which is not specified. Rather, the

qualitative outcomes of community members are valid for all CO₂ increment levels over which the assumptions underpinning the model are valid; namely, that the abundance of species linked to CO₂ can in fact be expressed as continuous functions of CO₂, and that the partial derivatives of those functions with respect to CO₂ can be well-represented by a linearization near equilibrium conditions (Puccia & Levins 1985, Levins 1998). If species responses to CO₂ are highly nonlinear or exhibit threshold behavior, such dynamics could be explored by developing and analyzing multiple QNMs (e.g. Dambacher & Ramos-Jiliberto 2007, Dambacher et al. 2009).

Linkage influence

We sought to identify linkages that strongly influenced the sign response of community members to OA (Melbourne-Thomas et al. 2012). To do so, we used Multivariate Adaptive Regression Splines (MARS) to evaluate relationships between the simulated interaction coefficients and the sign response of species composing the system (Reum et al. 2015). We specifically focused on assessing linkage influence on community responses to the press scenario in which OA simultaneously increased primary production and decreased bivalves (Scenario 4a, Table 1). To simplify analysis, we assumed no structural uncertainty in the model (Raymond et al. 2011). That is, all linkages, including those noted as uncertain, were retained in the network. Next, we simulated 1500 community matrices and calculated their associated

Table 1. Summary of the ocean acidification (OA) scenarios examined using qualitative network models of ecological interactions in Willapa Bay, Washington. For each scenario, the qualitative relationship (+ or -) linking the variable CO₂ to the respective community member is listed in the table column. Phyto: phytoplankton; Z.: *Zostera*. PI: predator interaction

Scenario code	Scenario	Primary producers			Bivalves		Enhanced drill-oyster PI		Enhanced red rock crab-oyster PI	
		Phyto	Z. <i>marina</i>	Z. <i>japonica</i>	Pacific oyster	Manila clam	Drills	Pacific oyster	Red rock crab	Pacific oyster
Primary producer	1a	(+)								
	1b		(+)							
	1c			(+)						
	1d		(+)	(+)						
	1e	(+)	(+)	(+)						
Bivalves	2a				(-)					
	2b					(-)				
	2c				(-)	(-)				
Enhanced predation	3a						(+)	(-)		
	3b								(+)	(-)
	3c						(+)	(-)	(+)	(-)
Combinations	4a (1e+2c)	(+)	(+)	(+)	(-)	(-)				
	4b (1e+3c)	(+)	(+)	(+)			(+)	(-)	(+)	(-)

press perturbation response to OA. For each community member, the sign outcome (+, -) was treated as a binomial response variable and the MARS model was fitted following Leathwick et al. (2005) and allowing for both first- and second-order interaction terms. Variables were retained if they reduced the residual squared error of the model by at least 0.01. For each fitted MARS model, the percentage of explained deviance associated with each retained predictor (i.e. the predictor's relative importance) was calculated (Milborrow 2014).

Last, we performed cluster analyses to identify community members with sign outcomes that were sensitive to similar sets of CO₂ linkages and identify CO₂ linkages that influenced similar sets of community members. Dendrograms were calculated from the relative importance of CO₂ linkages as estimated in the MARS models for each species based on the Bray-Curtis dissimilarity coefficient and the complete linkage clustering method (Legendre & Legendre 1998). Cluster analyses were performed using the library 'vegan' (Oksanen et al. 2013) and MARS models were fit using the statistical library 'earth' (Milborrow 2014) in the R v. 2.11 software program (R Core Team 2014).

RESULTS

Community responses across ocean acidification scenarios

The outcomes of several community members were nearly uniform across the different OA scenarios (Fig. 2). For instance, outcomes for the cultivated bivalve Manila clam were negative in 11 of the 13 scenarios, and 9 outcomes had high sign consistency (i.e. $\geq 70\%$; Fig. 2). For 3 of the 4 species of conservation or management concern (Chinook salmon, black brant, adult Dungeness crab), few negative outcomes were observed. Rather, black brant outcomes were positive in 10 of the 13 scenarios (8 had high sign consistency), Chinook salmon outcomes were all positive (3 had high sign consistency), and for adult Dungeness crab 10 of the 13 scenarios were also positive, but sign consistency was low in all scenarios (Fig. 2). The fourth species, green sturgeon, had net negative outcomes for most scenarios (10 of 13), but in all scenarios $>25\%$ of the simulated outcomes indicated no change in abundance (Fig. 2).

Among the primary producers, outcomes were positive across scenarios and generally showed high sign consistency, with only 2 and 3 exceptions for

Zostera marina and *Z. japonica*, respectively (Fig. 2). For the remaining species, outcomes for ghost shrimp were generally negative (10 out of 13 scenarios) while all outcomes for mud shrimp were positive and most (10 out of 13) showed high sign consistency (Fig. 2). For the group crows/gulls, the outcomes were negative in 11 scenarios, but in all scenarios no change in abundance was predicted in $>40\%$ of simulations (Fig. 2). Small fish, non-structure invertebrates, zooplankton, structure invertebrates, and drills had outcomes with high sign consistency in 2 or fewer scenarios (Fig. 2).

Within subsets of scenarios, tradeoffs between the cultivated bivalves or bivalves and other species of management and conservation concern were apparent. For instance, for all OA primary production scenarios (Scenarios 1a-d), Manila clam and Pacific oyster outcomes were opposite in sign (Fig. 2). Further, for the commercially fished Chinook salmon, positive outcomes with high sign consistency occurred in scenarios where the outcomes of one or both cultivated bivalve species were negative, and several scenarios indicated decreases in Manila clam and increases in black brant (Fig. 2).

In general, the community members that were directly affected by CO₂ had outcomes that were the same sign as the CO₂ interaction. However, the level of sign consistency changed for some species depending on the scenario. For Manila clam, direct CO₂ effects always resulted in negative responses with high sign consistency (Fig. 2), but for Pacific oyster, sign consistency was low when predation interactions were enhanced for red rock crab (Scenario 3b) and when the different categories of OA hypotheses were combined (Scenarios 4a and b). Similarly, outcomes for predators (drills and red rock crab) had low sign consistency in the categories where OA hypotheses were combined. All primary producers had outcomes with high sign consistency when directly stimulated by CO₂, with the exception of *Z. marina* when all 3 primary producers were pressed (Scenario 1e).

Linkage influence

A summary of the fitted MARS models that identified relationships between linkages and the sign response of community members is provided in Table 2. For all species, the proportion of negative responses from the simulated community interaction matrices ranged from 0.07 to 0.84, with an average of value of 0.48 (Table 2). The proportion of deviance in

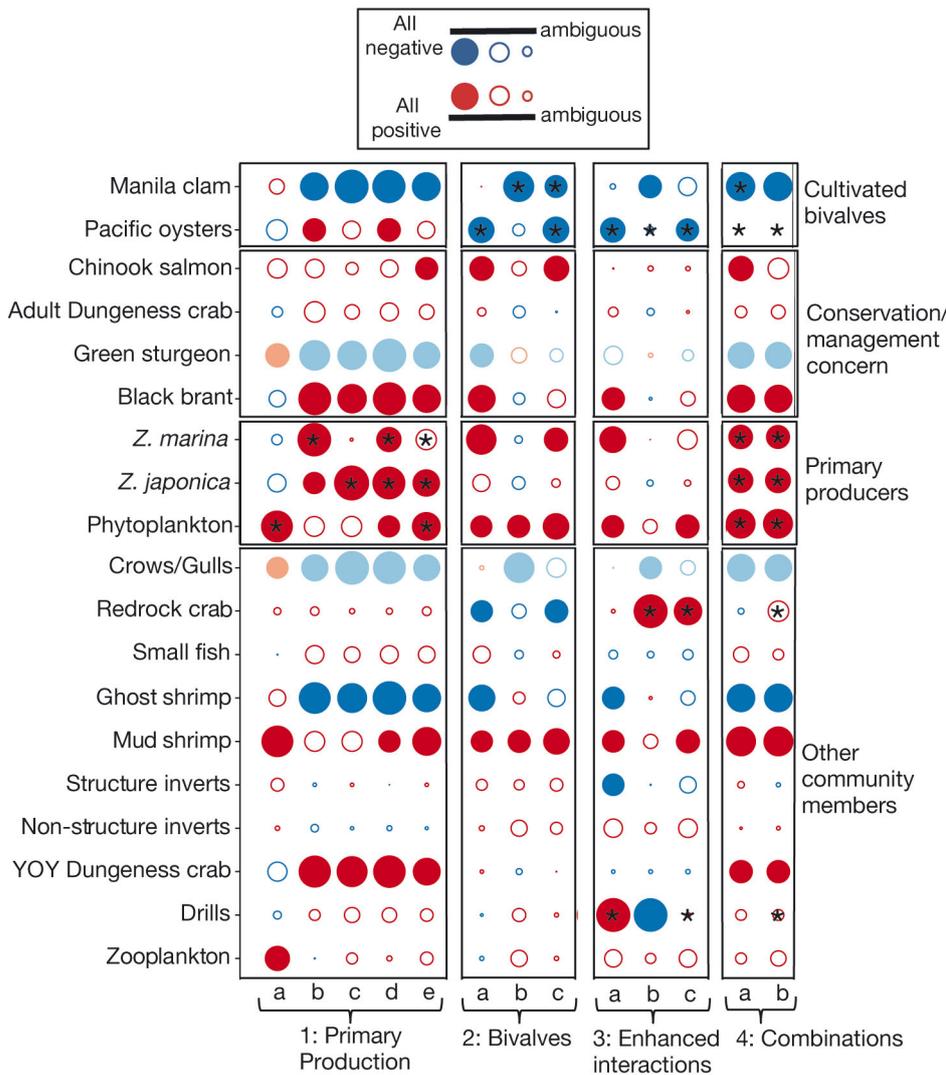


Fig. 2. Sign outcomes (positive or negative) of the Willapa Bay, Washington community to ocean acidification given different hypotheses of the effects of increased CO₂ on community members. Details of linkages between CO₂ and community members for each hypothesis scenario (1a–e, 2a–c, 3a–c, 4a,b) are provided in Table 1. Community member simulation outcomes to the CO₂ press for each scenario are coded red and blue for positive and negative, respectively. Circle size is proportional to the level of sign consistency; to aid interpretation, all outcomes with sign consistency >70% are solid, those <70% are open. For 2 community members (the group ‘Crows/Gulls’ and Green sturgeon), >40% of the simulated outcomes indicated no change in abundance (i.e. zero outcome); their symbol sizes reflect sign outcomes based on the non-zero simulated responses and are coded light blue and light red, to denote net negative and positive responses, respectively. Outcome symbols overlaid with an asterisk indicate community members linked directly to CO₂ in each OA scenario

the sign responses of community members explained by the MARS models was variable, ranging from 7 to 42% (Table 2). Of the 5 linkages that extended from CO₂ to community members, 1 to 4 linkages (average: 2.8) were identified as important predictors of

sign response; of the 65 community linkages (i.e. non-CO₂ linkages), between 4 and 14 linkages (average: 8.7) were included as predictors (Table 2).

The magnitude of interactions corresponding to linkages between CO₂ and phytoplankton, *Z. japonica*, *Z. marina*, Pacific oyster, and Manila clam were important to varying degrees in predicting sign responses in 16, 13, 11, 9, and 6 community members, respectively (Fig. 3). Overall, CO₂ linkages with the primary producers influenced the sign outcome of sets of community members that were more similar than those influenced by CO₂ linkages with Manila clam and Pacific oyster (Fig. 3). For instance, sign outcomes of ghost shrimp, green sturgeon, black brant, and young-of-the-year (YOY) Dungeness crab were all strongly influenced by CO₂ linkages to primary producers (Fig. 3). In general, CO₂ linkage with Manila clam and Pacific oyster influenced fewer community members overall (Fig. 3).

In addition to obtaining an overview of linkage influence for each community member, partial dependency plots of the fitted MARS models can be examined to evaluate how interaction magnitude influences the probability of a negative outcome for community members. For illustrative purposes, we focused on examining partial dependency plots for Pacific oyster, the bivalve species in the model that had the outcome with the lowest sign consistency (63% of responses were negative; Table 2). In total, 14 linkages were included in the Pacific oyster MARS model, but for brevity we present partial dependency plots for the 6 most important linkages in terms of deviance reduction. These linkages account

for ~70% of the explained deviance and include 3 linkages to CO₂, and 3 non-CO₂ linkages (Fig. 4a–f). As expected, the probability of a negative response in Pacific oyster increased with the strength of the negative CO₂-Pacific oyster interaction (Fig. 4a).

Table 2. Summary of Multivariate Adaptive Regression Spline (MARS) models predicting the simulated sign response (+, -) of Willapa Bay community members to Scenario 4a based on interaction coefficients corresponding to the linkages composing the network. All linkages denoted as uncertain in Fig. 1 were assumed to be certain. For each community member, the proportion of negative responses to the simulated press scenario is provided along with the deviance in the sign response explained by the MARS model. In the scenario, 5 linkages extended from CO₂ to community members and 65 linkages connected community members to each other (see Table 1 for details). For each community member, the number of linkages included as predictors that were directly connected to CO₂ and/or between community members in the network are indicated

Community member	Proportion (-)	% deviance explained	OA linkages (5 possible)	Non-OA linkages (65 possible)
<i>Z. japonica</i> ^a	0.28	42	2	9
Ghost shrimp	0.81	35	3	9
Green sturgeon	0.81	35	3	9
Black brant	0.19	31	4	10
Pacific oyster ^a	0.66	30	4	13
YOY Dungeness crab	0.27	29	4	12
Crows/Gulls	0.84	24	4	6
Manila clam ^a	0.84	24	4	6
<i>Z. marina</i> ^a	0.19	25	3	4
Zooplankton	0.45	23	2	11
Non-structure invertebrates	0.39	20	1	9
Structure invertebrates	0.38	19	2	14
Small fish	0.37	17	4	12
Adult Dungeness crab	0.46	17	4	10
Drills ^a	0.28	15	4	9
Mud shrimp	0.07	12	1	5
Phytoplankton ^a	0.07	12	1	5
Red rock crab ^a	0.78	12	2	9
Chinook salmon	0.11	7	3	4

^aCommunity members that are directly connected to CO₂ in the scenario

However, the probability decreased as the interaction strength between CO₂ and *Z. marina* and *Z. japonica* increased (Fig. 4b,c). Among the non-CO₂ interactions, negative responses were more likely when the *Z. marina*-ghost shrimp and ghost shrimp-Pacific oyster interactions were weak, and less likely when the phytoplankton-*Z. marina* interaction was weak (Fig. 4d-f).

DISCUSSION

Using a QNM, we showed how the direct effect of OA on one to several species potentially alters equilibrium abundances throughout the Willapa Bay community. By examining a variety of scenarios, we show that the sign outcome of some community members may be robust, thus helping to identify potential ‘winners’ and ‘losers’ despite uncertainty in the specific pathways through which OA may affect the community. Specifically, we showed that the cultivated species Manila clam responded negatively across most scenarios, while other community members, including

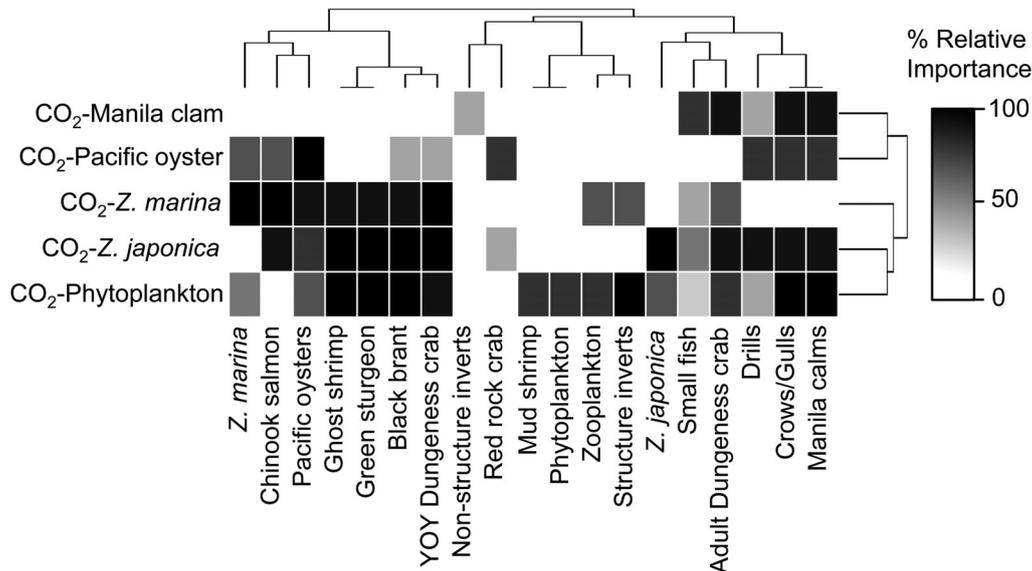


Fig. 3. Overview of the relative importance of CO₂ linkages in the Willapa Bay qualitative network model for predicting the sign outcome of community members (under Scenario 4a, Table 1) based on Multivariate Adaptive Regression Splines (MARS) models. Relative importance refers to the percent of explained deviance in the sign outcomes of community members that is associated with each linkage. Community members and linkages are both ordered according to similarity

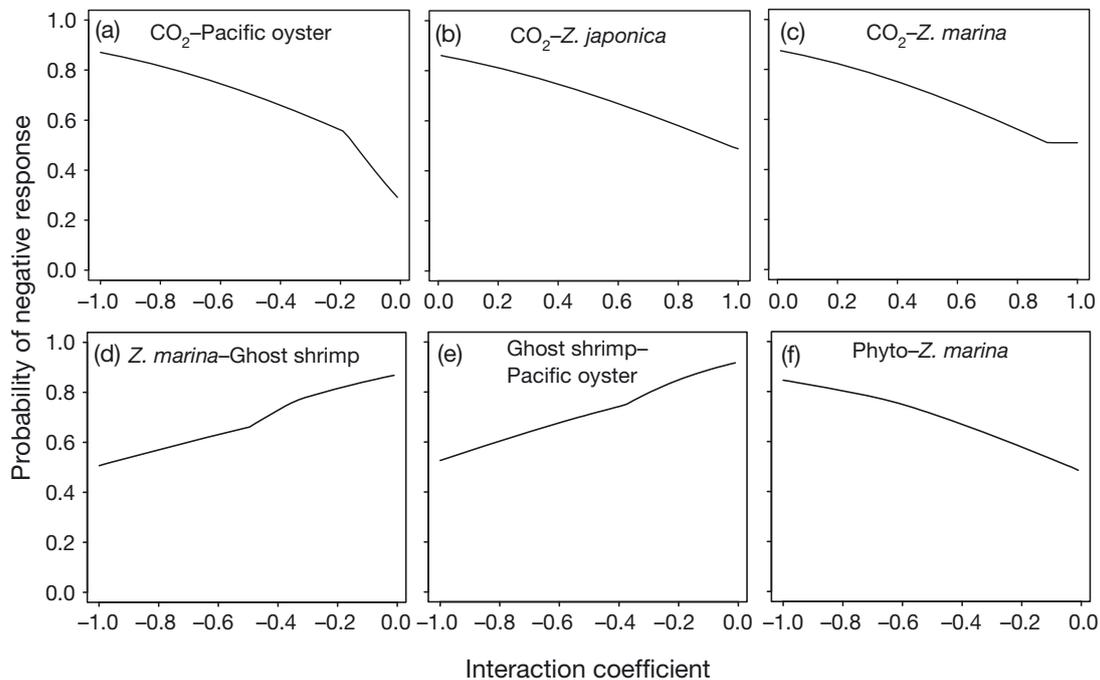


Fig. 4. Partial dependency plots of the probability of a negative response in the sign outcome of Pacific oyster under Scenario 4a (see Table 1) based on the fitted MARS model. The 6 variables account for ~70% of the deviance explained by the MARS model. Each panel indicates the probability of a negative response in the sign outcome of Pacific oyster as a function of the interaction strength of the respective linkage, while all other linkages included in the MARS model are set to their mean value

primary producers and species of management or conservation concern (e.g. Chinook salmon, black brant), tended to respond positively.

An important application of QNMs is that they can help identify tradeoffs resulting from environmental change or management actions (Dambacher et al. 2009, Carey et al. 2014). Importantly, we show that if OA effects are limited to changes in primary producers, Pacific oyster and Manila clam may exhibit opposite sign responses, reflecting their different placement in the network. An increase in eelgrass (*Z. japonica*) directly reduces Manila clam, but increases in eelgrass decrease ghost shrimp densities which, in turn, benefit Pacific oyster. Direct stimulation of eelgrass by CO_2 therefore has differing effects on the 2 bivalve species. Further, because phytoplankton negatively influences eelgrass through shading, an increase in phytoplankton alone can reverse the sign responses of the 2 bivalve species relative to the individual eelgrass stimulation scenarios. Other specific scenarios indicate potential tradeoffs between bivalves and the commercially fished Chinook salmon. For coastal economies dependent on fishing and aquaculture, QNMs may offer a practical tool for rapidly identifying potential resource responses to OA and thus where economic opportunity may contract or expand.

Our analysis of OA impacts within a community context using QNMs further underscores the need for caution when drawing inferences from single-species OA experiments to outcomes for wild populations. Generally, for community members directly linked to CO_2 , they responded in the same direction as the sign of the hypothesized direct CO_2 effect. However, responses tended to become ambiguous when direct CO_2 effects on multiple community members were considered simultaneously. For instance, under the scenario in which CO_2 affected only Pacific oyster, a decline in Pacific oyster was predicted (Scenario 2a). In more complex scenarios, including the scenarios in which multiple categories of hypothesized OA effects were pressed simultaneously (Scenario 4a,b) the response was ambiguous. The increase in ambiguity is caused by an increase in the number of countervailing feedback loops (Dambacher et al. 2003). That is, pathways conveying negative effects on Pacific oyster were partly canceled by pathways transmitting positive effects. The shift from high to low sign consistency indicates the importance of indirect pathways in mediating the response of some community members to OA. Because QNMs require as a minimum only information on the natural history of species composing a system (Levins 1998), they may be particularly relevant to researchers

as a simple method for identifying conditions under which the sign response of species to OA, as inferred from single-species OA experiments, will likely hold in the wild.

For complicated QNMs, statistical analysis of associations between the simulated interaction coefficients and the predicted response of species provides a simple approach for revealing key linkages and the manner in which they influence the likelihood of negative outcomes (Melbourne-Thomas et al. 2012, Reum et al. 2015). Under the scenario in which primary producers and both bivalve species were directly affected by CO₂ (Scenario 4a), the sign outcome of Pacific oyster showed low sign consistency (66%). The Pacific oyster MARS model showed that the sign was dependent primarily on a subset of interactions within the network. Unsurprisingly, the probability of observing a negative response increased with the negative interaction strength between CO₂ and Pacific oyster. The remaining linkages, however, indicate that the effect of CO₂ on eelgrasses is transmitted to Pacific oyster indirectly through a pathway that extends from eelgrass to ghost shrimp to Pacific oyster. Whether the interaction pathway is able to counteract the direct negative effects of OA on Pacific oyster will require additional quantitative information, and highlights an area to focus future research. In the same vein, systematic assessment of linkage influence for all community members identified interactions that were important community-wide. Among the hypothesized direct CO₂ effects in Willapa Bay, the CO₂-phytoplankton interaction was retained as a significant predictor for a majority of community members (84%), while the CO₂-manila clam linkage influenced the fewest (31%). Such information could help identify research priorities when considering the community as a whole.

Our analysis offers an initial evaluation of the potential effects of OA on the Willapa Bay community, but we emphasize that the model can easily be updated should new studies reveal important ecological interactions. Further, taxonomic and population-level variation in response to OA can be high (Parker et al. 2011, Kroeker et al. 2013a) and studies that are specific to Willapa Bay populations may identify new scenarios to investigate within the modeling framework or, alternatively, reduce the relevance of some of the scenarios we evaluated. In the case of eelgrass, field surveys of *Z. marina* growth along natural *p*CO₂ gradients in Willapa Bay suggest it may have a limited ability to respond positively to further increases in *p*CO₂ (Ruesink et al. 2015), though experiments

are needed to confirm this. The network configuration could also be adapted to address community interactions structured across space (e.g. Melbourne-Thomas et al. 2013), ontogenetic shifts in OA sensitivity and interspecific interactions (e.g. Whitlatch & Osman 1994), or more complex scenarios where OA is combined with other environmental stressors (e.g. warming, sea level rise, eutrophication, habitat loss, alteration of freshwater inputs; Kennish 2002, Scavia et al. 2002).

CONCLUSIONS

Models that incorporate interspecific interactions are recognized as necessary for understanding the potential effects of OA on natural communities, but so far have seen only limited use (Russell et al. 2012, Gaylord et al. 2015). We contend that this slow progress is related to several issues, some of which perhaps stem from an overemphasis on quantitative approaches to predicting OA effects. Quantitative models can offer more precise predictions relative to qualitative methods, but they also generally require a high degree of parameterization. Consequently, the need for additional data and the time and effort required to measure and estimate numerous parameters can be substantial. Furthermore, specifying quantitative relationships between the response variables measured in OA experiments and the vital rates that ultimately govern population growth or productivity is not always easy or feasible. For all but the most well-monitored and studied systems, the development of community-level quantitative models to evaluate OA impacts remains a major challenge and creates impediments with respect to management. We expect these issues will persist for some time given the usual limitations in data, time, and financial support for costly research and monitoring.

However, progress can be made in the meantime using qualitative approaches. As we demonstrate for Willapa Bay, QNMs can help synthesize the potential direct effects of OA on individual species and evaluate effects at the community level. QNMs allow investigators to move away from precise parameter estimation and specification of exact equations relating variables within the system. Instead, emphasis is placed on developing a robust conceptual model of how a system may work (Puccia & Levins 1985, Levins 1998). This approach helps to overcome some of the key challenges associated with applying quantitative models to OA. No single experimental or modeling approach is likely to capture all the com-

plex effects of OA on marine ecosystems, but the synthesis of findings from multiple approaches is likely to offer the most complete picture (Le Quesne & Pinnegar 2012). QNMs have received increased attention as alternatives or complements to quantitative methods and we suggest the approach may also have considerable value for understanding and predicting the effects of OA in marine communities.

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